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Phylogenetic classification of the world's tropical forests

J. W. Ferry Slik^{a,1}, Janet Franklin^{b,1}, Víctor Arroyo-Rodríguez^c, Richard Field^d, Salomon Aguilar^e, Nikolay Aguirre^f, Jorge Ahumada^g, Shin-Ichiro Aiba^h, Luciana F. Alvesⁱ, Anitha K^j, Andres Avella^k, Francisco Mora^c, Gerardo A. Aymard C.^{l,m}, Selene Báezⁿ, Patricia Balvanera^c, Meredith L. Bastian^o, Jean-François Bastin^p, Peter J. Bellingham^q, Eduardo van den Berg^r, Polyanna da Conceição Bispo^s, Pascal Boeckx^t, Katrin Boehning-Gaese^{u,v}, Frans Bongers^w, Brad Boyle^x, Fabian Brambach^y, Francis Q. Brearley^z, Sandra Brown^{aa,2}, Shauna-Lee Chai^{bb}, Robin L. Chazdon^{cc}, Shengbin Chen^{dd}, Phourin Chhang^{ee}, George Chuyong^{ff}, Corneille Ewango^{gg}, Indiana M. Coronado^{hh}, Jurgi Cristóbal-Azkarateⁱⁱ, Heike Culmsee^{jj}, Kipiro Damas^{kk}, H. S. Dattaraja^{ll}, Priya Davidar^{mm}, Saara J. DeWaltⁿⁿ, Hazimah Din^{oo}, Donald R. Drake^{oo}, Alvaro Duque^{pp}, Giselda Durigan^{qq}, Karl Eichhorn^{rr}, Eduardo Schmidt Eler^{ss}, Tsutomu Enoki^{tt}, Andreas Ensslin^{uu}, Adandé Belarmain Fandohan^{vv}, Nina Farwig^{ww}, Kenneth J. Feeley^{xx}, Markus Fischer^{uu}, Olle Forshed^{yy}, Queila Souza Garcia^{zz}, Satish Chandra Garkoti^{aaa}, Thomas W. Gillespie^{bbb}, Jean-François Gillet^{ccc}, Christelle Gonmadje^{ddd,eee}, Iñigo Granzow-de la Cerda^{fff}, Daniel M. Griffith^{ggg}, James Grogan^{hhh}, Khalid Rehman Hakeemⁱⁱⁱ, David J. Harris^{jjj}, Rhett D. Harrison^{kkk}, Andy Hector^{lll}, Andreas Hemp^{mmm}, Jürgen Homeierⁿⁿⁿ, M. Shah Hussain^{ooo}, Guillermo Ibarra-Manríquez^c, I. Faridah Hanum^{ppp}, Nobuo Imai^{qqq}, Patrick A. Jansen^{e,v}, Carlos Alfredo Joly^{rrr}, Shijo Joseph^{sss}, Kuswata Kartawinata^{ttt,uuu}, Elizabeth Kearsley^{vvv}, Daniel L. Kelly^{www}, Michael Kessler^{xxx}, Timothy J. Killeen^{yyy}, Robert M. Kooyman^{zzz,aaa}, Yves Laumonierⁱ, Susan G. Laurance^{bbb}, William F. Laurance^{bbb}, Michael J. Lawes^{ccc}, Susan G. Letcher^{ddd}, Jeremy Lindsell^{eee}, Jon Lovett^{fff,ggg}, Jose Lozada^{hhh}, Xinghui Luⁱⁱⁱ, Anne Mette Lykke^{jjj}, Khairil Bin Mahmud^{kkk}, Ni Putu Diana Mahayani^{lll}, Asyraf Mansor^{mmm,nnn}, Andrew R. Marshall^{ooo,ppp,qqq}, Emanuel H. Martin^{rrr}, Darley Calderado Leal Matos^{sss}, Jorge A. Meave^{ttt}, Felipe P. L. Melo^{uuu}, Zhofre Huberto Aguirre Mendoza^{vvv}, Faizah Metali^a, Vincent P. Medjibe^{www}, Jean Paul Metzger^{xxx}, Thiago Metzker^{zz,yyy}, D. Mohandass^{mm,zzz}, Miguel A. Munguía-Rosas^{aaaa}, Rodrigo Muñoz^{ttt}, Eddy Nurtjahy^{bbb}, Eddie Lenza de Oliveira^{cccc}, Onrizal^{ddd}, Pia Parolin^{eee,fff}, Marc Parren^{ggg}, N. Parthasarathy^{mm}, Ekananda Paudel^{hhh}, Rolando Perez^e, Eduardo A. Pérez-García^{ttt}, Ulf Pommer^u, Lourens Poorter^w, Lan Qie^{fff}, Maria Teresa F. Piedade^{ss}, José Roberto Rodrigues Pintoⁱⁱⁱ, Axel Dalberg Poulsen^{jjj}, John R. Poulsen^{jjj}, Jennifer S. Powers^{kkkk}, Rama Chandra Prasad^{llll}, Jean-Philippe Puyravaud^{mmmm}, Orlando Rangel^k, Jan Reitsmaⁿⁿⁿⁿ, Diogo S. B. Rocha^{oooo}, Samir Rolim^{pppp}, Francesco Rovero^{qqqq}, Andes Rozak^{rrrr}, Kalle Ruokolainen^{ssss}, Ervan Rutishauser^e, Gemma Rutten^{uu}, Mohd. Nizam Mohd. Said^{tttt}, Felipe Z. Saiter^{uuuu}, Philippe Saner^{vvvv}, Bráulio Santos^{wwwww}, João Roberto dos Santos^{xxxxx}, Swapnan Kumar Sarker^{yyyyy}, Christine B. Schmitt^{zzzzz,aaaaa}, Jochen Schoengart^{ss}, Mark Schulze^{bbbbb}, Douglas Sheil^{ccccc}, Plinio Sist^{ddddd}, Alexandre F. Souza^{eeeee}, Wilson Roberto Spironello^{ss}, Tereza Sposito^{zz,yyy}, Robert Steinmetz^{fffff}, Tariq Stevart^{ggggg}, Marcio Seiji Suganuma^{hhhhh}, Rahayu Sukri^a, Aisha Sultanaⁱⁱⁱⁱ, Raman Sukumar^{ll}, Terry Sunderland^j, Supriyadi^{lll}, H. S. Suresh^{ll}, Eizi Suzuki^h, Marcelo Tabarelli^{jjjj}, Jianwei Tang^{kkkkkk}, Ed V. J. Tanner^{llll}, Natalia Targhetta^{ss}, Ida Theilade^{mmmmmm}, Duncan Thomasⁿⁿⁿⁿⁿⁿ, Jonathan Timberlake^{gggg}, Márcio de Morisson Valeriano^{xxxxx}, Johan van Valkenburg^{ooooo}, Tran Van Do^{ppppp}, Hoang Van Sam^{qqqqq}, John H. Vandermeer^{rrrrr}, Hans Verbeeck^{vvv}, Ole Reidar Vetaas^{sssss}, Victor Adekunle^{ttttt}, Simone A. Vieira^{rrr}, Campbell O. Webb^{uuuuu}, Edward L. Webb^{vvvvv}, Timothy Whitfeld^{wwwwwww}, Serge Wich^{xxxxx,yyyyy}, John Williams^{zzzzz}, Susan Wiser^q, Florian Wittmann^{aaaaaaa}, Xiaobo Yang^{bbbbb}, C. Yves Adou Yao^{cccccc}, Sandra L. Yap^{ddddd}, Rakan A. Zahawi^{eeeeeee}, Rahmad Zakaria^{mmmm}, and Runguo Zangⁱⁱⁱⁱ

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¹To whom correspondence may be addressed. Email: ferryslik@hotmail.com or janet.franklin@ucr.edu.

²Deceased February 13, 2017.

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Knowledge about the biogeographic affinities of the world's tropical forests helps to better understand regional differences in forest structure, diversity, composition, and dynamics. Such understanding will enable anticipation of region-specific responses to global environmental change. Modern phylogenies, in combination with broad coverage of species inventory data, now allow for global biogeographic analyses that take species evolutionary distance into account. Here we present a classification of the world's tropical forests based on their phylogenetic similarity. We identify five principal floristic regions and their floristic relationships: (i) Indo-Pacific, (ii) Subtropical, (iii) African, (iv) American, and (v) Dry forests. Our results do not support the traditional neo- versus paleotropical forest division but instead separate the combined American and African forests from their Indo-Pacific counterparts. We also find indications for the existence of a global dry forest region, with representatives in America, Africa, Madagascar, and India. Additionally, a northern-hemisphere Subtropical forest region was identified with representatives in Asia and America, providing support for a link between Asian and American northern-hemisphere forests.

biogeographic legacies | forest classification | forest functional similarity | phylogenetic community distance | tropical forests

The biogeographic origin of species, in combination with dispersal limitation and environmental filtering, are the principal determinants of spatial variation in the species composition of tropical forests (1, 2). Despite evidence of long-distance dispersal (1, 3–5), tropical forests maintain conspicuous regional differences in species composition. For example, only ~4% of tropical tree species are shared among Africa, America, and Asia (6). The lack of species overlap among continents makes global inference of relationships among tropical forests problematic, because such classifications depend on comparison of the amount of shared species. Therefore, pan-tropical biogeographic analyses have been based on comparison of compositional patterns at higher taxonomic levels, namely genus or family (6–8). However, such analyses treat taxa as independent units, while in reality taxa vary in their degree of phylogenetic relatedness and, as a consequence, their morphological and ecological similarity (1, 2). Taking phylogenetic relatedness into consideration enhances our ability to delimit phytogeographical boundaries that characterize functional and biogeographic affinities among forest regions (1, 2, 9, 10). Here we include phylogenetic relationships in a floristic analysis to provide such insight.

We compiled a standardized dataset of old-growth tropical forest inventories of angiosperm trees (trunk diameter ≥ 10 cm) for 406 1° latitude/longitude grid cells (hereafter referred to as “locations”) originally dominated by natural forests across the (sub)tropics (Table S1). These locations represented all major tropical forest regions and had broad environmental amplitude, including low to high elevations and dry to wet forests (Fig. 1 and Fig. S1). To determine the phylogenetic distance between locations, we constructed a dated phylogenetic tree that was resolved to genus level and contained all taxa used for our classification analyses (Dataset S1). Location pairwise phylogenetic distance matrices were constructed using 20 randomly drawn tree taxa per location. We used 20 taxa, as this maximized the number of locations that could be included in the classification analyses while still providing a reliable classification result. In total, we generated 20 phylogenetic distance matrices, each with a different set of 20 randomly drawn taxa per location, which served as input for 20 cluster analyses (Fig. S2). The final classification of each location depended on the frequency with which it was classified in a particular cluster across all 20 cluster analyses (Fig. S3). Relationships between the clusters were represented by a majority rule consensus tree (Fig. 1).

Significance

Identifying and explaining regional differences in tropical forest dynamics, structure, diversity, and composition are critical for anticipating region-specific responses to global environmental change. Floristic classifications are of fundamental importance for these efforts. Here we provide a global tropical forest classification that is explicitly based on community evolutionary similarity, resulting in identification of five major tropical forest regions and their relationships: (i) Indo-Pacific, (ii) Subtropical, (iii) African, (iv) American, and (v) Dry forests. African and American forests are grouped, reflecting their former western Gondwanan connection, while Indo-Pacific forests range from eastern Africa and Madagascar to Australia and the Pacific. The connection between northern-hemisphere Asian and American forests is confirmed, while Dry forests are identified as a single tropical biome.

Results and Discussion

Mean pairwise phylogenetic distance analysis, which emphasizes ancient lineages in phylogenetic community comparisons, detected almost no spatial patterns in community phylogenetic similarity across the tropics, indicating that all tropical forest locations consist of more or less the same set of ancient plant lineages. This is in accordance with recent findings that the whole present-day tropics are dominated by similar high levels of Late Cretaceous aged phylogenetic lineages (11). Only when we used mean nearest taxon distance, which emphasizes recent lineages in phylogenetic community comparisons, did we detect clear spatial patterns across the tropics. Therefore, current-day biogeographic patterns in the tropics seem to mainly reflect Cenozoic speciation events when Gondwanan breakup was already well on its way.

Using the mean nearest taxon distance, our phylogenetic cluster analyses showed that the world's tropical forests are divided into two major floristic regions: a combined American-African versus Indo-Pacific region (Fig. 1). This division contradicts previous hypotheses about major global realms, which either recognized neo- versus paleotropical regions or several separate continental regions (4, 12–14). However, Gentry (7) already noted the high generic-level similarity of tropical American and African forests. He attributed this to Cretaceous and Cenozoic plate tectonic history (4, 15). Subsequent studies have shown that despite the severing of direct land connections between the African and South American plates ca. 96 Mya, long-distance dispersal continued throughout the Late Cretaceous and Early Tertiary across the widening Atlantic Ocean (4, 5). The combined effect of shared origin with trans-Atlantic migration may explain the detected connection between South American and African forests.

Within the American-African cluster, the first split separated the African from the American regions (Fig. 1), suggestive of the west Gondwanan breakup associated with the formation of the Atlantic Ocean and, over time, the increasing difficulty for plants to disperse across the Atlantic (1, 15). Interestingly, the African region showed the highest consistency in clustering of all five identified floristic regions. On average, locations belonging to the African region were assigned to this cluster in 91.4% of cases, versus consistency values of 79.5, 63.7, 79.5, and 70.3% for the Indo-Pacific, Subtropical, American, and Dry forest regions, respectively. This clustering consistency indicates high floristic similarity across tropical Africa, which is in accord with the relatively low beta diversity observed for these forests (6). Postulated repeated cycles of contraction and expansion of the tropical African forests from a few small forest refugia in combination

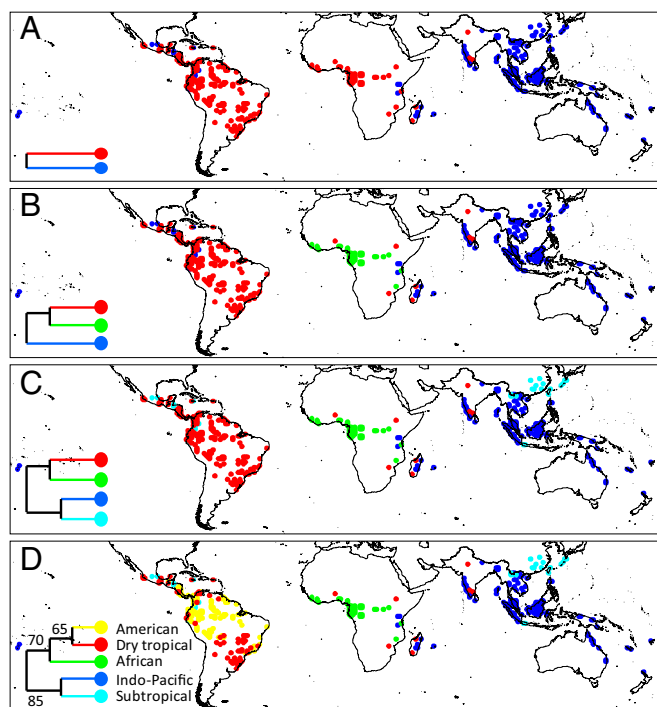


Fig. 1. Classification maps of the world's tropical forests, showing two (A), three (B), four (C), and five (D) clusters. Cluster result represents a majority rule consensus tree, with the percentage of times that each grouping was observed in the 20 separate cluster analyses shown in D. Only locations that could be classified with certainty ($P < 0.05$) are shown ($n = 392$).

with large-scale species shifts during the Pleistocene glaciations may explain the relatively high compositional homogeneity of the forests within the African region (16, 17).

The tropical American forests were further divided into moist and dry forests (Fig. 1 and Fig. S1), indicating that this division is primarily environmental (18). The American floristic region comprises humid forests, including the lowland forests of Central America, the Amazon basin, the Guianas, and the northern half of the Atlantic forest. The Dry forest region encompasses the Caatinga and Cerrado regions as well as other dry forests throughout the Americas but interestingly, and contrary to the nonphylogenetic pan-tropical analysis by Dexter et al. (8), also includes dry forests of Africa, Madagascar, and India. Further research is needed to confirm whether this indicates the existence of a global dry forest region with a shared biogeographic origin, or whether selection for drought and fire resistance has favored the dominance of similar plant lineages in tropical dry forests around the world (8, 18, 19).

The Indo-Pacific floristic region occupies the humid areas of eastern Africa, Madagascar, India, Southeast Asia, Australia, and the Pacific Islands (Fig. 1). With the exception of SE Asia, which is of Laurasian origin, this floristic region combines all areas that once comprised eastern Gondwana (4, 15). Given the diverse geologic history of Asia and the Indo-Pacific (20), it is surprising to find a similar forest type covering most of the region. Nevertheless, there is strong evidence of significant plant migration within this region that likely had a homogenizing effect, notably the biotic exchange between India and Southeast Asia starting from ca. 45 Mya (21), and between Southeast Asia and Australia, New Guinea, and the Pacific Islands that commenced ca. 15 Mya (4). The presence of Indo-Pacific forests in eastern continental Africa may either reflect eastern Gondwanan origin or dispersal within the Indo-Pacific region.

We also identified a group of locations in Asia and America that occupies cooler climates and higher elevations relative to the other identified forest clusters (Fig. 1 and Fig. S1), and which we therefore termed the Subtropical region. This Subtropical floristic region confirms the floristic link between Asia and North America, reflecting a shared boreotropical affinity (22). Within Asia, the Subtropical region is mostly restricted to the subtropics, with the exception of high-elevation forests of Java. In the Americas, by contrast, this floristic region extends from the subtropics deep into the tropics, probably because the cooler montane climate of the Central American highlands and South American Andes has facilitated the southward migration of cold-adapted plant lineages. The absence of continuous, North-South-oriented mountain chains in Asia may have limited the dispersal of such lineages into lower latitudes.

Conclusion

We provide a phylogenetic distance-based biogeographic classification of the world's tropical forests, using the most extensive sampling scheme for the tropics currently in existence. Our results uncover floristic patterns which will help in the development of region-specific models for forest structure, diversity, and dynamics as well as possible responses of tropical forest regions to global environmental change. Our results may necessitate reconsideration of established biogeographic ideas. For example, Madagascar and New Guinea have often been considered two separate major tropical regions, ecologically and biogeographically distinct from tropical America, Africa, and Southeast Asia (23, 24). However, despite their highly endemic species compositions, we show that they are both part of the widespread Indo-Pacific floristic region. Finally, our analysis can serve as a model for classifying regional floras.

Materials and Methods

Tree Inventory Dataset. Individual angiosperm trees (diameter at breast height ≥ 10 cm) from old-growth forest inventories throughout the (sub)tropics (between -35°S and 35°N latitudes) were pooled within their respective 1° latitude/longitude grid cells (henceforth called locations). These locations represented all major tropical forest regions and had broad environmental amplitude, including low to high elevations and dry to wet forests (Fig. S1). Monocots and Cactaceae were excluded because these were not consistently surveyed in all datasets. This dataset originally included 439 locations containing 925,009 individual trees belonging to 15,012 taxa. Species names were standardized using The Plant List (www.theplantlist.org), Taxonomic Name Resolution Service (tnrs.iplantcollaborative.org/TNRSapp.html), and Asian Plant Synonym Lookup (phylodiversity.net/fslik/synonym_lookup.htm). On average, 1.4% of individual stems per location remained unidentified. These unidentified individuals were excluded from further analyses.

Community Phylogenetic Tree. The APG-III classification (25) served as the family-level backbone of our community phylogenetic tree. Recent updates in APG-IV (26) are mostly of nomenclatural nature and did not affect our analyses. This tree was further resolved up to genus level using the species-level phylogeny (32,223 species included) published by Zanne et al. (27), which covered most genera in our dataset (Dataset S1). Genera present in our dataset, but not in Zanne et al. (27), were placed at the base of their respective families. Genera that had disjunct species occurrences in the phylogeny of Zanne et al. (27) were placed at the most basal node connecting the disjunct species. This phylogeny was subsequently dated using the BLADJ function in Phylocom v4.2 (28), using taxon ages given in Magallón et al. (29) for the age file.

Phylogenetic Distance Analysis. Phylogenetic distance between all pairs of locations was calculated using the options COMDIST and COMDISTNT in Phylocom v4.2 (28). COMDIST uses the mean pairwise phylogenetic distance (MPPD); for each taxon in a location, it finds the average phylogenetic distance to all taxa in the other location, and calculates the mean. COMDISTNT uses the mean nearest taxon distance (MNTD); for each taxon in location 1, it finds the nearest phylogenetic neighbor in location 2, records this, and calculates the mean. Both functions return a symmetrical matrix of locations

versus locations with their pairwise phylogenetic distances. Principal coordinate (PCO) analyses (in MultiVariate Statistical Package v3.13; Kovach Computing Services) on resulting location versus location matrices showed that the MPPD matrices had almost no explanatory power (generally the first five PCO axes explained less than 5% of data variance), meaning that detected patterns were mostly random. The MNTD matrices, however, explained considerable amounts of data variance in the first five axes of the PCO. Therefore, we used only MNTD for further analysis.

Correcting for Taxon Richness Bias in MNTD. Taxon richness differed considerably between locations, varying between 4 and 1,466. MNTD may be sensitive to such differences in taxon richness because the chance of finding a close relative between two locations may increase when their taxon richness increases. Applying MNTD to determine phylogenetic distance between locations with differing taxon numbers could therefore result in taxon-rich locations being grouped together in the cluster analysis simply because they are more taxon-rich. To determine the impact of this effect, we created five “location-by-taxon” matrices, each with a lower number of taxa per location (320, 160, 80, 40, and 20 taxa per location), using the 41 locations containing more than 320 taxa. For each location, taxa were ranked according to abundance, so that the location-by-taxon matrix based on, for example, 320 taxa consisted only of the 320 most abundant taxa per location. Where tied abundances exceeded the predefined number of taxa, we randomly selected the appropriate number of taxa from among those with tied minimum abundance. We then calculated the MNTD matrices for each of these five location-by-taxon matrices and found that with increasing taxon richness of locations, MNTD (as averaged over all locations) decreased with increasing taxon richness per location following a power function [$y = 310.4x^{-0.194}$ (Fig. S4)], demonstrating that MNTD is indeed sensitive to taxon richness.

Determining the Optimal Number of Taxa per Location for Further Analysis. To avoid taxon richness bias when using MNTD, locations had to be compared based on similar numbers of taxa. Minimum variance clustering, based on the five location-by-taxon matrices described earlier, consistently recovered the same major clusters in the same configuration (African and American locations clustered on one main branch and Asian locations clustered on the other), although the relationships between locations within these main clusters could vary (Fig. S5). Only in the 20-taxon analysis was one American location (location no. 165 from the Brazilian Atlantic Forest) placed in the Asian cluster. The amount of variance captured in the first five axes of a PCO analysis (using the same MNTD matrices) declined by only ~20%, from 83.3 to 60.7%, between the 320- and 20-taxon analyses, respectively. We decided to use 20 taxa per location in the final analyses (Table S1) because of this limited loss of information in the PCO and similarity of cluster results. In addition, we were able to use most of our locations (406 of the initial 439), including locations on remote islands and extreme habitats that would have been excluded if we had set the minimum number of taxa too high.

Forest Classification Analyses. For the final analyses, we produced 20 location-by-taxon datasets. In these datasets, each location was represented by 20 randomly drawn taxa (from that location). Random draws were irrespective of taxon abundance, as abundance is a spatially and temporally labile taxon trait that likely reflects contemporary environmental conditions rather than historical biogeographic signal. For each of these 20 location-by-taxon datasets, we calculated the corresponding symmetrical location-by-location matrices with their pairwise phylogenetic distances (MNTD). These matrices were then used as input for cluster analyses.

Locations were grouped in clusters using Ward’s minimum variance method (30), using MultiVariate Statistical Package v3.13. This is a centroid-based clustering technique that identifies cluster centers (centroids) by minimizing the overall squared distances of the objects (in this case locations) to the

centroids at each cluster level. This clustering technique identified spatially clearly defined location groupings (Fig. S2). The optimal number of clusters for defining floristic regions across the tropics was determined by calculating the cophenetic correlation coefficient at each cluster level, starting at the first split (K2) in the dendrogram. The cophenetic correlation coefficient calculates the correlation between the distance of the clusters as calculated by the clustering algorithm and the distance based on observed MNTD values between clusters. The higher the cophenetic correlation, the better the cluster result reflects the patterns present in the original distance matrix. We applied this method to each of our 20 datasets, calculated the average cophenetic correlation coefficient for each cluster level, and found a steep increase in cophenetic correlation up to K5, after which it slowly declined (Fig. S6). Therefore, we chose K5 as the optimum level for defining our main floristic regions across the tropics.

For each location, at cluster level K5, we determined the cluster in which it was classified for each of the 20 cluster analyses that we performed. The location was then assigned to the cluster in which it had the highest proportion of observations. A single proportion test (31), which calculates the probability of an observed (sample) proportion (in the range 0 to 1) against a hypothetical proportion, was then used to determine if the observed proportions were significantly higher than expected by random [Paleontological Statistics (PAST) v3.08; <https://folk.uio.no/ohammer/past/>]. For example, for K5, the expected random proportion of locations per cluster is 0.2. For a sample size of 20, a proportion has to be at least 0.38 to be significantly higher ($P < 0.05$) than the random expectation. The resulting classification success rates of locations for K5 are shown in Fig. S3 and Table S1. The final classification (K5) of the clusters was based on the majority consensus rule (Fig. 1).

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^aEnvironmental and Life Sciences, Faculty of Science, Universiti Brunei Darussalam, Gadong BE1410, Brunei Darussalam; ^bDepartment of Botany and Plant Sciences, University of California, Riverside, CA 92521; ^cInstituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, 58190 Morelia, Michoacán, México; ^dSchool of Geography, University of Nottingham, Nottingham NG7 2RD, United Kingdom; ^eCenter for Tropical Forest Science, Smithsonian Tropical Research Institute, Ancon, Panama; ^fBiodiversity and Ecosystem Services Research Program, Universidad Nacional de Loja, Loja EC110103, Ecuador; ^gThe Moore Center for Science, Conservation International, Arlington, VA 22202; ^hGraduate School of Science and Engineering, Kagoshima University, Kagoshima 890-0065, Japan; ⁱCenter for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles, CA 90095; ^jForest and Environment Program, Center for International Forestry Research (CIFOR), Bogor 16115, Indonesia; ^kInstituto de Ciencias Naturales, Universidad Nacional de Colombia, Sede Bogotá 111321, Colombia; ^lUNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, Estado Portuguesa 3350, Venezuela; ^mCompensation International Progress S.A.–Ciprogress Greenlife, Bogotá D.C., Colombia; ⁿDepartamento de Biología, Escuela Politécnica Nacional del Ecuador, Ladrón de Guevara E11-253, Quito, Ecuador; ^oSmithsonian’s National Zoo, Animal Care Sciences, Primates, Washington, DC 20013-7012; ^pInstitute of Integrative Biology, Department of Environmental Systems Science, ETH Zurich, 8092 Zurich, Switzerland; ^qLandcare Research Manaaki Whenua, Lincoln 7640, New Zealand; ^rDepartamento de Biología, Universidade Federal de Lavras, Lavras-MG, 37200-000, Brazil; ^sCentre for Landscape and Climate

Research, Department of Geography, University of Leicester, Leicester LE1 7RH, United Kingdom; ¹Isotope Bioscience Laboratory (ISOFLYS), Department of Green Chemistry and Technology, Faculty of Bioscience Engineering, Ghent University, B-9000 Ghent, Belgium; ²Senckenberg Biodiversity and Climate Research Centre (BiK-F), 60325 Frankfurt (Main), Germany; ³Institute for Ecology, Evolution and Diversity, Goethe University Frankfurt, 60439 Frankfurt (Main), Germany; ⁴Forest Ecology and Forest Management Group, Wageningen University & Research, 6700 AA Wageningen, The Netherlands; ⁵Hardner & Gullison Associates, Victoria, BC V8P 1A9, Canada; ⁶Ecology and Ecosystem Research, Georg August University Göttingen, 37073 Göttingen, Germany; ⁷School of Science and the Environment, Manchester Metropolitan University, Manchester M1 5GD, United Kingdom; ^{8a}Environment Group, Winrock International, St Dogmaels SA43 3 DT, United Kingdom; ^{8b}Ecosystem Management Unit, InnoTech Alberta, Vegreville, AB T9C 1T4, Canada; ⁹Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043; ¹⁰College of Environment and Ecology, Chengdu University of Technology, Chengdu 610059, China; ¹¹Forest and Wildlife Research Institute, 12101 Phnom Penh, Cambodia; ¹²Department of Botany and Plant Physiology, University of Buea, POB 63 Buea, Cameroon; ¹³Wildlife Conservation Society-Program DR Congo, B.P. 14537 Brazzaville, DR Congo; ¹⁴Departamento de Biología, Facultad de Ciencias y Tecnología, Universidad Nacional Autónoma de Nicaragua, Herbario HULE, León 505, Nicaragua; ¹⁵Division of Biological Anthropology, University of Cambridge, Cambridge CB2 3QG, United Kingdom; ¹⁶DBU Natural Heritage, German Federal Foundation for the Environment, 49090 Osnabrück, Germany; ¹⁷PNG Forest Research Institute, Lae 411, Morobe Province, Papua New Guinea; ¹⁸Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India; ¹⁹Department of Ecology and Environmental Sciences, Pondicherry University, Puducherry 605014, India; ²⁰Department of Biological Sciences, Clemson University, Clemson, SC 29634; ²¹Botany Department, University of Hawaii, Honolulu, HI 96822; ²²Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Medellín, Colombia; ²³Laboratório de Ecologia e Hidrologia Florestal, Floresta Estadual de Assis, Instituto Florestal de SP, 19802-970 Assis, SP, Brazil; ²⁴Eichhorn Ecologie, 3702 BK Zeist, The Netherlands; ²⁵Instituto Nacional de Pesquisas da Amazônia-INPA, Araújo, CEP 69067-375 Manaus AM, Brazil; ²⁶Kasuya Research Forest, Kyushu University, Sasaguri, Fukuoka 811-2415, Japan; ²⁷Institute of Plant Sciences, University of Bern, 3013 Bern, Switzerland; ²⁸Ecole de Foresterie et Ingénierie du Bois, Université Nationale d'Agriculture, BP 45, Kétou, Benin; ²⁹Conservation Ecology, Faculty of Biology, Philippos-Universität Marburg, 35032 Marburg, Germany; ³⁰Department of Biology, University of Miami, Coral Gables, FL 33146; ³¹WWF-Sweden/Världsnaturfonden WWF, Ulriksdals Slott, S-170 81 Solna, Sweden; ³²Departamento de Botânica, Universidade Federal de Minas Gerais, Pampulha, 31270-901 Belo Horizonte, Minas Gerais, Brazil; ^{33a}School of Environmental Sciences, Jawaharlal Nehru University, New Delhi 110067, India; ^{33b}Department of Geography, University of California, Los Angeles, CA 90095; ³⁴TERRA Teaching and Research Center, Central African Forests, Gembloux Agro-Bio Tech, University of Liège, B-5030 Gembloux, Belgium; ³⁵Department of Plant Biology, Faculty of Sciences, University of Yaounde I, Yaounde, BP 812, Cameroon; ³⁶National Herbarium, Yaoundé, BP 20818, Cameroon; ³⁷CREAF, Universitat Autònoma de Barcelona, Cerdanyola del Vallès 08193, Spain; ³⁸Universidad Técnica Particular de Loja, Loja 1101608, Ecuador; ³⁹Mount Holyoke College Botanic Garden, South Hadley, MA 01075; ⁴⁰Department of Biological Sciences, Faculty of Science, King Abdulaziz University, Jeddah 21589, Saudi Arabia; ⁴¹Royal Botanic Garden Edinburgh, Edinburgh EH3 5LR, United Kingdom; ⁴²World Agroforestry Centre, East and Southern Africa Region, Woodlands, Lusaka, Zambia; ⁴³Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, United Kingdom; ⁴⁴Department of Plant Systematics, University of Bayreuth, 95440 Bayreuth, Germany; ⁴⁵Plant Ecology, Albrecht von Haller Institute of Plant Sciences, Georg August University Göttingen, 37073 Göttingen, Germany; ⁴⁶Biodiversity Parks Programme, Centre for Environmental Management of Degraded Ecosystems, University of Delhi, Delhi 110007, India; ⁴⁷Faculty of Forestry, Universiti Putra Malaysia, Serdang-43400, Selangor, Malaysia; ^{48a}Department of Forest Science, Tokyo University of Agriculture, Tokyo 156-8502, Japan; ^{48b}UNICAMP, Cidade Universitária Zeferino Vaz-Barão Geraldo, Campinas, Sao Paulo 13083-970, Brazil; ⁴⁹Geographic Information Systems and Remote Sensing Department, Kerala Forest Research Institute, Peechi, Kerala 680653, India; ⁵⁰Integrative Research Center, The Field Museum, Chicago, IL 60605; ⁵¹Herbarium Bogoriense, Research Center for Biology, Indonesian Institute of Sciences, Cibinong 16911, Indonesia; ⁵²Computational and Applied Vegetation Ecology (CAVElab), Department of Environment, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, B-9000 Ghent, Belgium; ⁵³Trinity Centre for Biodiversity Research, Trinity College, The University of Dublin, Dublin 2, Ireland; ⁵⁴Department of Systematic and Evolutionary Botany, University of Zurich, 8008 Zurich, Switzerland; ⁵⁵Agteca-Amazonica, Santa Cruz, Bolivia; ⁵⁶Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia; ^{57a}National Herbarium of New South Wales, Royal Botanic Gardens and Domain Trust, Sydney, NSW 2000, Australia; ^{57b}Centre for Tropical Environmental and Sustainable Science and College of Science and Engineering, James Cook University, Cairns, QLD 4878, Australia; ⁵⁸School of Life Sciences, University of KwaZulu-Natal, Scottsville 3209, South Africa; ⁵⁹Department of Plant Biology, College of the Atlantic, Bar Harbor, ME 04609; ⁶⁰The RSPB Centre for Conservation Science, Sandy, Bedfordshire SG19 2DL, United Kingdom; ⁶¹School of Geography, University of Leeds, Leeds LS2 9JT, United Kingdom; ⁶²Herbarium, Royal Botanic Gardens Kew, Richmond, Surrey TW9 3AB, United Kingdom; ⁶³Facultad de Ciencias Forestales y Ambientales, Universidad de los Andes, Merida 5101-A, Venezuela; ⁶⁴Key Laboratory of Forest Ecology and Environment of State Forestry Administration, Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China; ⁶⁵Department of Bioscience, Aarhus University, 8600 Silkeborg, Denmark; ⁶⁶Faculty of Bioresources and Food Sciences, Universiti Sultan Zainal Abidin, 20300, Besut Campus, Terengganu, Malaysia; ⁶⁷Faculty of Forestry, Universitas Gadjah Mada, Yogyakarta 55281, Indonesia; ⁶⁸School of Biological Sciences, Universiti Sains Malaysia, 11800 Penang, Malaysia; ⁶⁹Centre for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 Penang, Malaysia; ⁷⁰CIRCLE, University of York, York YO10 5NG, United Kingdom; ⁷¹Flamingo Land, North Yorkshire YO17 6UX, United Kingdom; ⁷²Tropical Forests and People Research Centre, University of the Sunshine Coast, QLD 4556, Australia; ⁷³College of African Wildlife Management, Department of Wildlife Management, Moshi, Tanzania; ⁷⁴Museu Paraense Emílio Goeldi, Belém PA, 66040-170, Brazil; ⁷⁵Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, C.P. 04510, Mexico; ⁷⁶Center for Biosciences, Federal University of Pernambuco, Cidade Universitária, Recife PE, 50670-901, Brazil; ⁷⁷Herbario Loja, Universidad Nacional de Loja, Loja EC110103, Ecuador; ⁷⁸Commission des Forêts d'Afrique Centrale (COMIFAC), BP 20818 Yaoundé, Cameroon; ⁷⁹Department of Ecology, Institute of Bioscience, University of São Paulo, 05508-900 São Paulo, SP, Brazil; ⁸⁰Programa de Pós-Graduação em Ecologia, Conservação e Manejo da Vida Silvestre (ECMVS), IBAM-Instituto Bem Ambiental, Belo Horizonte-Minas Gerais, 30360-310, Brazil; ⁸¹Root and Soil Biology Laboratory, Department of Botany, Bharathiar University, Coimbatore 641 046, India; ^{82a}Laboratorio de Ecología Terrestre, Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional (CINVESTAV), C.P. 927310 Mérida, México; ^{82b}Department of Biology, Universitas Bangka Belitung (UBB), Kampus Merawang, Kepulauan Bangka Belitung 33172, Indonesia; ⁸³Programa de Pós Graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso-UNEMAT, 78200-000 Cáceres, Mato Grosso, Brazil; ⁸⁴Faculty of Forestry, Universitas Sumatera Utara, Medan 20155, Indonesia; ⁸⁵Department of Biodiversity, Evolution and Ecology of Plants, Biocentre Klein Flottbek, University of Hamburg, D-22609 Hamburg, Germany; ⁸⁶Institut Sophia Agrobiotech, 06903 Sophia Antipolis Cedex, France; ⁸⁷World Resource Institute, Washington, DC 20002; ⁸⁸Centre for Mountain Ecosystem Studies, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China; ⁸⁹Departamento de Engenharia Florestal, Universidade de Brasília, 70910-900, Brasília, Distrito Federal, Brazil; ⁹⁰Nicholas School of the Environment, Duke University, Durham, NC 27708; ⁹¹College of Biological Sciences, University of Minnesota, St. Paul, MN 55108; ⁹²International Institute of Information Technology, Gachibowli, Hyderabad, Telangana 500032, India; ⁹³Sigur Nature Trust, Chadapatti, Masinagudi PO Nilgiris, TN 643223, India; ⁹⁴Bureau Waardenburg, 4100 AJ Culemborg, The Netherlands; ⁹⁵Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Estadual de Santa Cruz, Ilhéus, Bahia 45662-900, Brazil; ⁹⁶Laboratório de Restinga e Floresta Atlântica, Universidade Federal do Espírito Santo, BR-101 São Mateus, Brazil; ⁹⁷Tropical Biodiversity Section, MUSE - Museo delle Scienze, 38122 Trento, Italy; ⁹⁸Cibodas Botanic Gardens, Indonesian Institute of Sciences (LIPI), Cipanas, Cianjur, West Java 43253, Indonesia; ⁹⁹Department of Geography and Geology, University of Turku, Turku, 20014 Turun yliopisto, Finland; ¹⁰⁰School of Environmental and Natural Resource Sciences, Faculty of Science and Technology, Universiti Kebangsaan Malaysia, 43600 UKM Bangi, Selangor, Malaysia; ¹⁰¹Instituto Federal de Educação, Ciência e Tecnologia do Espírito Santo, São João de Petrópolis, Santa Teresa, 29660-000, Brazil; ¹⁰²Department of Evolutionary Biology and Environmental Studies, University of Zurich, CH-8057 Zurich, Switzerland; ¹⁰³Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, 58051-900, Brazil; ¹⁰⁴Remote Sensing Department (DSR), National Institute for Space Research (INPE), São José dos Campos, São Paulo 12227-010, Brazil; ¹⁰⁵Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow G12 8QQ, United Kingdom; ¹⁰⁶Center for Development Research (ZEF), University of Bonn, 53113 Bonn, Germany; ¹⁰⁷Chair of Nature Conservation and Landscape Ecology, University of Freiburg, 79085 Freiburg im Breisgau, Germany; ¹⁰⁸H.J. Andrews Experimental Forest, Blue River, OR 97413; ¹⁰⁹Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, 1432 Ås, Norway; ¹¹⁰Cirad-ES, Campus International de Baillarguet, TA C-105/D 34398 Montpellier Cedex 5, France; ¹¹¹Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Natal, CEP 59078-970, Brazil; ¹¹²World Wildlife Fund Thailand, Bangkok 10400, Thailand; ¹¹³Africa and Madagascar Department, Missouri Botanical Garden, St. Louis, MO 63110; ¹¹⁴Federal University of Technology-Paraná, 86812-460, Apucarana,

Academy of Sciences, Menglun Town, Mengla County, Yunnan Province 666303, China; ⁱⁱⁱⁱⁱⁱDepartment of Plant Sciences, University of Cambridge, Cambridge CB2 3EA, United Kingdom; ^{mmmmmm}Department of Food and Resource Economics, University of Copenhagen, 1165 Copenhagen, Denmark; ⁿⁿⁿⁿⁿⁿDepartment of Biological Sciences, Washington State University, Vancouver, WA 98686; ^{oooooo}Netherlands Food and Consumer Product Safety, Authority, National Reference Centre, 6700HC Wageningen, The Netherlands; ^{pppppp}Research Institute for Sustainable Humanosphere, Kyoto University, Uji, Kyoto 611-0011, Japan; ^{qqqqqq}Science, Technology and International Cooperation Department, Vietnam National University of Forestry, Hanoi 144, Vietnam; ^{rrrrrr}Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109; ^{ssssss}Department of Geography, University of Bergen, N-5020 Bergen, Norway; ^{tttttt}Department of Forestry and Wood Technology, The Federal University of Technology, P.M.B. 704 Akure, Nigeria; ^{uuuuuu}Arnold Arboretum, Harvard University, Boston, MA 02130; ^{vvvvvv}Department of Biological Sciences, National University of Singapore, Singapore 117543, Singapore; ^{wwwwww}Brown University, Providence, RI 02912; ^{xxxxxx}School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool L3 3AF, United Kingdom; ^{yyyyyy}Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1098 Amsterdam, The Netherlands; ^{zzzzzz}Instituto Politécnico Nacional, CIIDIR-Unidad Oaxaca, Santa Cruz Xoxocotlán, CP 71230, Oaxaca, Mexico; ^{aaaaaa}Department of Floodplain Ecology, Institute of Geography and Geoecology, Karlsruhe Institute of Technology, D-76437 Rastatt, Germany; ^{bbbbbb}College of Agriculture and Forestry, Hainan University, Meilan Qu Haikou Shi, 570228, Hainan Province, China; ^{cccccc}Biosciences, Université Félix Houphouët-Boigny, Abidjan 22, Ivory Coast; ^{ddddd}Institute of Arts and Sciences, Far Eastern University, Manila, Philippines; and ^{eeeeee}Department of Biology, American University of Beirut, Riad El-Solh, Beirut 1107 2020, Lebanon

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Correction

ECOLOGY

Correction for “Phylogenetic classification of the world’s tropical forests,” by J. W. Ferry Slik, Janet Franklin, Víctor Arroyo-Rodríguez, Richard Field, Salomon Aguilar, Nikolay Aguirre, Jorge Ahumada, Shin-Ichiro Aiba, Luciana F. Alves, Anitha K, Andres Avella, Francisco Mora, Gerardo A. Aymard C., Selene Báez, Patricia Balvanera, Meredith L. Bastian, Jean-François Bastin, Peter J. Bellingham, Eduardo van den Berg, Polyanna da Conceição Bispo, Pascal Boeckx, Katrin Boehning-Gaese, Frans Bongers, Brad Boyle, Fabian Brambach, Francis Q. Brearley, Sandra Brown, Shauna-Lee Chai, Robin L. Chazdon, Shengbin Chen, Phourin Chhang, George Chuyong, Corneille Ewango, Indiana M. Coronado, Jurgi Cristóbal-Azkarate, Heike Culmsee, Kipiro Damas, H. S. Dattaraja, Priya Davidar, Saara J. DeWalt, Hazimah Din, Donald R. Drake, Alvaro Duque, Giselda Durigan, Karl Eichhorn, Eduardo Schmidt Eler, Tsutomu Enoki, Andreas Ensslin, Adandé Belarmain Fandohan, Nina Farwig, Kenneth J. Feeley, Markus Fischer, Olle Forshed, Queila Souza Garcia, Satish Chandra Garkoti, Thomas W. Gillespie, Jean-François Gillet, Christelle Gonmadje, Iñigo Granzow-de la Cerda, Daniel M. Griffith, James Grogan, Khalid Rehman Hakeem, David J. Harris, Rhett D. Harrison, Andy Hector, Andreas Hemp, Jürgen Homeier, M. Shah Hussain, Guillermo Ibarra-Manríquez, I. Faridah Hanum, Nobuo Imai, Patrick A. Jansen, Carlos Alfredo Joly, Shijo Joseph, Kuswata Kartawinata, Elizabeth Kearsley, Daniel L. Kelly, Michael Kessler, Timothy J. Killeen, Robert M. Kooyman, Yves Laumonier, Susan G. Laurance, William F. Laurance, Michael J. Lawes, Susan G. Letcher, Jeremy Lindsell, Jon Lovett, Jose Lozada, Xinghui Lu, Anne Mette Lykke, Khairil Bin Mahmud, Ni Putu Diana Mahayani, Asyraf Mansor, Andrew R. Marshall, Emanuel H. Martin, Darley Calderado Leal Matos, Jorge A. Meave, Felipe P. L.

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The authors note that, due to a printer’s error, an author name published incorrectly. The author name Lan Qi should instead appear as Lan Qie. The online version has been corrected.

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